

THE MAYFIELD METHOD OF ESTIMATING NESTING SUCCESS: A MODEL, ESTIMATORS AND SIMULATION RESULTS

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Mayfield (1960, 1961, 1975) proposed a method of estimating nesting success which removes potential sources of bias often associated with other estimates of this parameter. Despite the intuitive appeal of Mayfield's method and the general recognition that it is appropriate (e.g., Miller and Johnson 1978, Custer and Pitelka 1977, Johnson 1979), it is still not widely used. In this paper we present a probabilistic model for the experimental situation considered by Mayfield (1960, 1961, 1975). We then obtain maximum likelihood estimators based on this model and present results of Monte Carlo simulations designed to evaluate the estimators. Sample size considerations are also discussed.

Mayfield's method is based on the concept of "nest days." The model he employs assumes the following: (a) the complete period to success, which we will call the nesting period, (for example, the period of incubation of eggs) is the same number of days, say J days, for all nests; (b) there is a constant unknown probability, p ($0 < p < 1$), over this period that a nest observed on day j will survive to day $j + 1$; the probability of a nest succeeding from day 1 to full term is then p^J ; (c) there is a fixed unknown probability, θ_j , that an observed nest will have been first found on day j of the nesting period of J days (for $j = 1, 2, \dots, J$).

Assume that we observe K nests under the above model. For each of these nests we observe a random vector $X_k = (Y_k, T_k)$, $k = 1, 2, \dots, K$, where (i) Y_k is a random variable taking the value 1 if the k^{th} nest is successful (i.e., survives the complete nesting period) and the value 0 if the nest fails at any time, and (ii) T_k is a random variable denoting the number of days the k^{th} nest is observed until it either succeeds or fails. For example, an observation of (0, 10) would mean a nest was seen on 10 days but on the 11th day visit it had failed, while a value of (1, 10) would mean a nest was seen on 10 days and on the 11th day was observed to have succeeded (for example, hatchlings were present on day 11). Given the random vectors X_1, \dots, X_K we wish to estimate p , the daily probability of survival.

To do this we consider the joint distribution of (Y_k, T_k) :

$$(1) \quad f(y, t|p) = [\theta_{J-t+1}p^t]^y \left[p^{t-1}(1-p) \prod_{j=1}^{J-t+1} \theta_j \right]^{1-y}$$

TABLE 1
RESULTS OF MONTE CARLO SIMULATIONS DESIGNED TO EVALUATE THE MAXIMUM LIKELIHOOD ESTIMATORS FOR DAILY SURVIVAL PROBABILITY AND ITS VARIANCE^a

J	P	p ^j	1/l(p)	K	Mean estimated values					Actual confidence interval coverage				
					\hat{p}	\hat{p}^j	\hat{v}	Ks ²	\bar{Y}	Max \hat{p}	Min \hat{p}	90%	95%	99%
10	0.750	0.056	0.0551	20	0.741	0.050	0.0536	0.0586	0.152	0.850	0.526	0.90	0.95	0.99
				75	0.750	0.056	0.0270	0.0551	0.152	0.843	0.688	0.91	0.95	0.99
				500	0.751	0.057	0.0105	0.0548	0.152	0.773	0.728	0.92	0.95	1.00
10	0.850	0.197	0.0302	20	0.849	0.195	0.0387	0.0307	0.369	0.931	0.750	0.93	0.96	0.98
				75	0.846	0.188	0.0204	0.0315	0.363	0.890	0.789	0.87	0.91	1.00
				500	0.849	0.195	0.0078	0.0305	0.367	0.873	0.827	0.89	0.94	0.97
10	0.900	0.349	0.0194	20	0.901	0.353	0.0308	0.0197	0.547	0.972	0.750	0.87	0.94	0.96
				75	0.899	0.345	0.0161	0.0198	0.539	0.936	0.855	0.87	0.94	0.99
				500	0.902	0.357	0.0062	0.0190	0.539	0.915	0.886	0.89	0.94	0.99
10	0.950	0.599	0.0094	20	0.947	0.580	0.0221	0.0103	0.739	0.989	0.896	0.90	0.94	0.97
				75	0.952	0.611	0.0109	0.0090	0.758	0.974	0.919	0.84	0.92	0.98
				500	0.950	0.599	0.0043	0.0095	0.744	0.959	0.938	0.95	0.98	1.00
20	0.850	0.039	0.0218	20	0.847	0.036	0.0336	0.0231	0.131	0.913	0.736	0.93	0.95	0.98
				75	0.847	0.036	0.0173	0.0225	0.120	0.890	0.799	0.93	0.97	0.99
				500	0.850	0.039	0.0066	0.0218	0.122	0.864	0.830	0.93	0.95	0.99
20	0.900	0.122	0.0124	20	0.899	0.119	0.0251	0.0132	0.288	0.957	0.754	0.83	0.88	0.96
				75	0.899	0.119	0.0129	0.0127	0.277	0.929	0.862	0.89	0.92	0.99
				500	0.901	0.124	0.0050	0.0123	0.280	0.912	0.885	0.88	0.93	0.96

TABLE 1
CONTINUED

J	p	p ^j	1/(p)	K	Mean estimated values					Actual confidence interval coverage				
					\hat{p}	\hat{p}^j	\hat{v}	K \hat{v}^2	\bar{Y}	Max \hat{p}	Min \hat{p}	90%	95%	99%
20	0.950	0.358	0.0054	20	0.948	0.344	0.0166	0.0058	0.554	0.980	0.903	0.84	0.90	0.96
				75	0.949	0.351	0.0086	0.0056	0.558	0.967	0.928	0.90	0.95	0.99
				500	0.950	0.358	0.0033	0.0055	0.558	0.958	0.943	0.89	0.94	1.00
20	0.970	0.544	0.0031	20	0.969	0.533	0.0125	0.0033	0.712	0.995	0.931	0.91	0.95	0.98
				75	0.970	0.544	0.0064	0.0032	0.715	0.985	0.957	0.91	0.96	0.97
				500	0.970	0.544	0.0025	0.0030	0.718	0.976	0.965	0.90	0.95	1.00
20	0.990	0.818	0.0010	20	0.991	0.835	0.0066	0.0010	0.913	1.000	0.973	0.79	0.84	1.00
				75	0.990	0.818	0.0035	0.0010	0.900	0.998	0.982	0.92	0.95	0.98
				500	0.990	0.818	0.0014	0.0010	0.898	0.993	0.987	0.90	0.97	0.99
30	0.900	0.042	0.0104	20	0.893	0.034	0.0240	0.0119	0.129	0.953	0.820	0.89	0.95	0.99
				75	0.899	0.041	0.0118	0.0106	0.135	0.927	0.860	0.89	0.93	0.97
				500	0.900	0.042	0.0045	0.0103	0.131	0.910	0.891	0.92	0.98	1.00
30	0.950	0.215	0.0040	20	0.948	0.201	0.0146	0.0044	0.398	0.978	0.895	0.90	0.93	0.98
				75	0.949	0.208	0.0074	0.0042	0.403	0.971	0.930	0.86	0.88	0.98
				500	0.950	0.215	0.0028	0.0040	0.411	0.957	0.942	0.91	0.97	0.99
30	0.970	0.401	0.0022	20	0.968	0.377	0.0109	0.0025	0.594	0.997	0.944	0.93	0.96	0.98
				75	0.969	0.389	0.0055	0.0023	0.600	0.981	0.952	0.90	0.94	0.99
				500	0.970	0.401	0.0021	0.0022	0.603	0.976	0.964	0.90	0.95	0.98

TABLE I
CONTINUED

J	p	p ^j	1/l(p)	K	Mean estimated values					Actual confidence interval coverage				
					\hat{p}	\hat{p}^j	\hat{v}	K ²	\bar{Y}	Max \hat{p}	Min \hat{p}	90%	95%	99%
30	0.990	0.740	0.0007	20	0.990	0.740	0.0058	0.0007	0.848	1.000	0.969	0.79	0.86	0.97
				75	0.990	0.740	0.0029	0.0007	0.857	0.997	0.982	0.87	0.91	0.96
				500	0.990	0.740	0.0011	0.0007	0.854	0.993	0.987	0.86	0.90	0.96
30	0.995	0.860	0.0003	20	0.995	0.860	0.0043	0.0004	0.925	1.000	0.984	0.96	0.99	1.00
				75	0.995	0.860	0.0021	0.0003	0.925	0.999	0.986	0.88	0.91	0.93
				500	0.995	0.860	0.0008	0.0003	0.925	0.997	0.993	0.88	0.95	0.99
40	0.950	0.129	0.0034	20	0.949	0.123	0.0132	0.0036	0.293	0.972	0.905	0.89	0.95	0.91
				75	0.950	0.129	0.0067	0.0034	0.301	0.963	0.933	0.90	0.96	1.00
				500	0.950	0.129	0.0026	0.0034	0.294	0.955	0.942	0.87	0.92	0.99
40	0.970	0.296	0.0018	20	0.967	0.261	0.0098	0.0020	0.482	0.989	0.942	0.91	0.93	0.97
				75	0.969	0.284	0.0049	0.0018	0.503	0.981	0.955	0.87	0.93	0.98
				500	0.970	0.296	0.0019	0.0018	0.507	0.974	0.967	0.95	0.98	1.00
40	0.990	0.669	0.0005	20	0.990	0.669	0.0055	0.0011	0.806	1.000	0.971	0.86	0.88	0.95
				75	0.990	0.669	0.0026	0.0005	0.811	0.996	0.983	0.87	0.96	0.98
				500	0.990	0.669	0.0010	0.0005	0.805	0.992	0.987	0.88	0.96	0.99
40	0.995	0.818	0.0003	20	0.995	0.818	0.0096	0.0064	0.898	1.000	0.984	0.99	1.00	1.00
				75	0.995	0.818	0.0018	0.0003	0.903	0.999	0.989	0.83	0.90	0.95
				500	0.995	0.818	0.0007	0.0003	0.901	0.996	0.993	0.91	0.94	1.00

^a All estimates are based on 100 simulations. J represents the entire nesting period; p and \hat{p} are the true and estimated values of daily survival probability; p^j and \hat{p}^j are the true and estimated probabilities of a new nest surviving the entire nesting period and succeeding; 1/l(p) and K² are the true and estimated variances of \sqrt{K} (p-p); \sqrt{JK} (p) and \hat{v} are the true and estimated asymptotic standard deviations of \hat{p} ; K denotes the number of nests observed; \bar{Y} denotes the observed proportion of nests which is successful.

for $y = 0, 1$ and $t = 1, 2, \dots, J$.

The log likelihood function (see Cramér 1946:498–506) for our random sample is:

$$(2) \quad \log \prod_{k=1}^K \left[\theta_{J-T_k+1} \right]^{Y_k} + \left[\sum_{k=1}^K T_k Y_k \right] \log p \\ + \sum_{k=1}^K (T_k - 1)(1 - Y_k) \log p + \left(K - \sum_{k=1}^K Y_k \right) \log(1 - p) \\ + \log \prod_{k=1}^K \left[\sum_{j=1}^{J-T_k+1} \theta_j \right]^{1-Y_k}.$$

Differentiating (2) with respect to p , setting the derivative equal to zero and solving for p , yields the maximum likelihood estimate (m.l.e.) of p , say \hat{p} (see Cramér 1946:498–506). Here we have

$$(3) \quad \hat{p} = \frac{\sum_{k=1}^K T_k + \sum_{k=1}^K Y_k - K}{\sum_{k=1}^K T_k}.$$

Mayfield (1960, 1961, 1975) proposes the following estimator for p : Count the total number of nest days observed (i.e., $\sum_{k=1}^K T_k$); count the total number of failures (i.e., $K - \sum_{k=1}^K Y_k$), and estimate p by

$$\frac{1 - K - \sum_{k=1}^K Y_k}{\sum_{k=1}^K T_k} \text{ which is in fact } \hat{p}, \text{ the m.l.e.}$$

The theory of maximum likelihood yields that the asymptotic distribution of $\sqrt{K}(\hat{p} - p)$ is Normal with mean zero and variance $1/I(p)$ where $I(p)$ is the Fisher information and

$$I(p) = -E \left[\frac{\partial^2 \log f(Y, T|p)}{\partial p^2} \right]$$

(see Cramér 1946:498–506). As usual, E denotes expected value. Thus, the asymptotic variance of \hat{p} is

$$(4) \quad \frac{1}{K I(p)} = \frac{1}{K} \frac{p^2(1-p)^2}{ET(1-p)^2 + (EY - 1)(1-2p)}$$

which we can estimate as

$$\hat{v}^2 = \begin{cases} \frac{\frac{1}{(K)} \hat{p}^2(1 - \hat{p})^2}{\bar{T}(1 - \hat{p})^2 + (\bar{Y} - 1)(1 - 2\hat{p})} = \frac{\hat{p}(1 - \hat{p})}{K \bar{T}} & \text{if } \bar{Y} \neq 1 \\ \frac{1}{K \bar{T}} & \text{if } \bar{Y} = 1. \end{cases}$$

Here \bar{T} and \bar{Y} denote the sample means of T and Y , respectively. Approximate $1 - \alpha$ confidence intervals for p are then given by

$$(\hat{p} - z_{\alpha/2} \hat{v}, \hat{p} + z_{\alpha/2} \hat{v})$$

where $z_{\alpha/2}$ is the upper $\alpha/2$ value for the standard normal distribution,

$$\text{i.e., } \int_{-\infty}^{z_{\alpha/2}} \frac{1}{\sqrt{2\pi}} \exp(-z^2/2) dz = 1 - \alpha/2.$$

Similarly, approximate level α tests for the equality of p values from 2 populations of nests are given by the following: reject H_0 , the null hypothesis that $p_1 = p_2$, in favor of the alternative hypothesis that $p_1 \neq p_2$ if and only if

$$(5) \quad \frac{|\hat{p}_1 - \hat{p}_2|}{\sqrt{\hat{v}_1^2 + \hat{v}_2^2}} > z_{\alpha/2}.$$

The behavior of these confidence intervals and tests depends on the efficacy of \bar{T} , \bar{Y} , and \hat{p} as estimators of ET , EY and p respectively. To investigate this behavior we performed Monte Carlo simulations of a nesting experiment which met the assumptions of our model. We chose several values of J (nesting period), K (the number of observed nests) and p (the daily survival probability). The θ_j probabilities were chosen to be in proportion to the available number of nests from the j^{th} day of nesting given that the same number of new nests are started each day and only p of them survive to the second day, p^2 to the third, etc.; i.e.,

$$\text{we set } \theta_j = \frac{p^{j-1}(1 - p)}{1 - p^J}, \quad j = 1, 2, \dots, J.$$

We randomly divided the K nests into J groups using the distribution given by the θ_j values. Each nest from the j^{th} group was then followed until it survived for $J - j + 1$ days or until it failed. The probability of daily survival was p , and the probability of full term success for a nest for J days was p^J . The appropriate (Y, T) vector was recorded for each of the K nests, and \hat{p} , \hat{v} , and estimated confidence intervals (90%, 95%, 99%) were calculated. It was then determined whether or not the computed

TABLE 2
RESULTS OF SIMULATIONS INVESTIGATING THE POWER OF THE SUGGESTED TEST STATISTIC, $|\hat{p}_1 - \hat{p}_2| / \sqrt{\hat{v}_1^2 + \hat{v}_2^2}^a$

J	p _t	K	λ																
			-0.040	-0.030	-0.020	-0.010	-0.005	-0.001	0.0	0.001	0.005	0.010	0.020	0.030	0.040				
----- Proportion of the times null hypothesis was rejected at the $\begin{pmatrix} \alpha = 0.10 \\ \alpha = 0.05 \\ \alpha = 0.01 \end{pmatrix}$ significance levels -----																			
10	0.95	20	0.37	0.23	0.16	0.14	0.13	0.08	0.09	0.09	0.09	0.13	0.15	0.30	0.31				
			0.21	0.13	0.07	0.04	0.06	0.03	0.06	0.03	0.05	0.06	0.05	0.12	0.16				
			0.07	0.06	0.01	0.00	0.00	0.01	0.00	0.01	0.00	0.01	0.01	0.00	0.01	0.01			
20	0.95	75	0.77	0.45	0.37	0.17	0.11	0.10	0.09	0.19	0.11	0.15	0.48	0.80	0.93				
			0.69	0.33	0.25	0.10	0.06	0.05	0.04	0.11	0.05	0.09	0.32	0.70	0.89				
			0.45	0.14	0.09	0.03	0.01	0.00	0.00	0.04	0.01	0.02	0.05	0.38	0.78				
500	0.95	500	1.00	1.00	0.91	0.43	0.26	0.07	0.08	0.08	0.25	0.56	0.99	1.00	1.00				
			1.00	0.99	0.86	0.35	0.15	0.01	0.04	0.02	0.14	0.38	0.98	1.00	1.00				
			1.00	0.95	0.67	0.11	0.04	0.00	0.01	0.00	0.07	0.18	0.88	1.00	1.00				
20	0.95	20	0.40	0.34	0.19	0.10	0.11	0.05	0.06	0.10	0.07	0.14	0.32	0.42	0.76				
			0.26	0.24	0.13	0.06	0.07	0.00	0.02	0.08	0.05	0.06	0.21	0.30	0.67				
			0.10	0.09	0.02	0.00	0.02	0.00	0.00	0.00	0.01	0.01	0.04	0.09	0.26				
75	0.95	75	0.88	0.70	0.46	0.17	0.15	0.06	0.11	0.12	0.10	0.21	0.60	0.92	0.99				
			0.82	0.58	0.38	0.10	0.10	0.04	0.03	0.06	0.04	0.10	0.48	0.92	0.99				
			0.57	0.29	0.16	0.03	0.03	0.00	0.00	0.00	0.02	0.02	0.28	0.75	0.96				
500	0.95	500	1.00	1.00	0.99	0.61	0.28	0.10	0.11	0.09	0.35	0.74	1.00	1.00	1.00				
			1.00	1.00	0.99	0.50	0.19	0.09	0.04	0.05	0.28	0.68	0.99	1.00	1.00				
			1.00	1.00	0.92	0.26	0.08	0.01	0.01	0.02	0.06	0.37	0.99	1.00	1.00				

TABLE 2
CONTINUED

J	p ₁	K	Δ													
			-0.040	-0.030	-0.020	-0.010	-0.005	-0.001	0.0	0.001	0.005	0.010	0.020	0.030	0.040	
30	0.95	20	0.54	0.34	0.28	0.08	0.07	0.07	0.09	0.11	0.11	0.18	0.37	0.57	0.83	
			0.33	0.23	0.15	0.05	0.03	0.03	0.06	0.07	0.07	0.07	0.12	0.21	0.47	0.80
			0.10	0.07	0.02	0.00	0.01	0.00	0.01	0.01	0.01	0.01	0.00	0.09	0.22	0.55
40	0.99	20	0.96	0.78	0.58	0.25	0.08	0.08	0.11	0.03	0.19	0.33	0.79	0.98	1.00	
			0.88	0.70	0.39	0.17	0.04	0.01	0.07	0.02	0.09	0.18	0.65	0.98	1.00	
			0.66	0.40	0.19	0.05	0.00	0.00	0.03	0.01	0.01	0.06	0.37	0.88	1.00	
500	0.99	20	1.00	1.00	0.99	0.74	0.27	0.07	0.14	0.09	0.34	0.88	1.00	1.00		
			1.00	1.00	0.99	0.69	0.20	0.02	0.08	0.07	0.23	0.83	1.00	1.00		
			1.00	1.00	0.98	0.43	0.09	0.00	0.03	0.00	0.11	0.64	1.00	1.00		
75	0.99	20	0.94	0.81	0.66	0.36	0.14	0.10	0.09	0.11	0.09	— ^b	—	—		
			0.90	0.73	0.49	0.24	0.07	0.01	0.03	0.05	0.03	—	—	—		
			0.66	0.39	0.21	0.03	0.02	0.00	0.01	0.00	0.00	—	—	—		
500	0.99	20	1.00	1.00	0.98	0.66	0.29	0.15	0.09	0.11	0.39	—	—	—		
			1.00	1.00	0.97	0.55	0.20	0.06	0.05	0.05	0.29	—	—	—		
			1.00	0.99	0.87	0.31	0.04	0.01	0.02	0.02	0.17	—	—	—		
75	0.99	20	1.00	1.00	1.00	1.00	0.95	0.15	0.15	0.24	1.00	—	—	—		
			1.00	1.00	1.00	1.00	0.87	0.09	0.08	0.16	1.00	—	—	—		
			1.00	1.00	1.00	1.00	0.69	0.03	0.01	0.05	0.94	—	—	—		

^a 100 simulations were conducted for each combination of J, p₁, K and Δ values. In each simulation, 2 groups of nests characterized by p₁ and p₂ (where p₂ = p₁ + Δ) were sampled and p₁, p₁, p₂ and \hat{v}_2 estimated. The proportion of these simulations in which the null hypothesis (p₁ = p₂) is rejected is presented (for Δ = 0 this estimates the significance level of the test). J denotes the nesting period and K is the number of nests observed for both of the simulated groups. Results are presented for 3 significance levels (α = 0.10, 0.05, 0.01) for each set of simulations.

^b For p₁ = 0.99, values of Δ ≥ 0.01 are not biologically reasonable. Thus, values for Δ ≥ 0.01 are not presented.

confidence intervals contained the true value of p . The entire above procedure was repeated 100 times for each combination of J , p and K values. We computed the proportion of the 100 times in which the estimated confidence interval in fact covered the true value. We also determined the mean, minimum and maximum values of the 100 estimates of p , the mean value of the 100 estimates \hat{v} and the mean of the 100 estimates $K\hat{v}^2$ (which should estimate $1/I(p)$). These values are compared with the theoretical values, p , $1/I(p)$, and the exact confidence proportions, in Table 1. The means of the estimated values \hat{p} and $K\hat{v}^2$ appeared to be good estimators of p and $1/I(p)$ in virtually all simulated cases. In addition, the actual confidence interval coverages were close to the theoretical values, especially when it is remembered that proportions represent results of only 100 simulations.

We also calculated \hat{p}^J as an estimate of $p^J = p^J$, the probability of full term success. An alternative estimate of p^J , which is commonly used in nesting studies, is $\bar{Y} = \sum_{k=1}^K Y_k/K$, the ratio of the number of observed successful nests to total observed nests. The comparisons of \hat{p}^J and \bar{Y} as estimates of p^J show the superiority of \hat{p}^J in cases where the model assumptions are met (Table 1).

All of the results presented in Table 1 were obtained assuming

$$\theta_j = \frac{p^{j-1}(1-p)}{1-p^j}, \quad j = 1, 2, \dots, J.$$

In order to assess the robustness of the above procedures to changes in this assumption we set all θ_j equal (i.e., $\theta_j = 1/J$, $j = 1, 2, \dots, J$) and conducted additional simulations for many of the situations examined in Table 1. Results were virtually identical to those presented in Table 1, indicating that the estimators are quite robust with respect to reasonable changes in the θ_j values.

In addition, we ran Monte Carlo simulations of tests of equality of two p values using the test statistic in (5). We assessed both type I and type II error probabilities under several experimental situations. These results are presented in Table 2 and can be used as empirical approximations to the power of these hypothesis tests under various conditions. It should be noted that the power curve is not symmetric. Thus, for a specified value of Δ a test of the null hypothesis that $p_1 = p_2$ given that $p_2 = p_1 + \Delta$ (for $p_1 > 0.5$) is more powerful for $\Delta > 0$ than for $\Delta < 0$.

We note that the estimator \hat{v}^2 can be useful in planning an experiment in which the daily survival probability is to be estimated. If we express the desired precision of \hat{p} in terms of a specific coefficient of variation, cv (where $cv = v/p$), then we can substitute estimates or guesses for p , ET , EY

TABLE 3
 SAMPLE SIZES (NUMBER OF NESTS) NEEDED TO ESTIMATE DAILY SURVIVAL PROBABILITY (P) WITH SPECIFIED LEVELS OF PRECISION^a

Nesting period (J)	Daily survival probability (p)	Desired coefficient of variation (v/p)					
		0.050	0.040	0.030	0.020	0.010	0.005
		Sample size					
10	0.75	39	61	109	245	980	3918
10	0.85	—	26	47	105	419	1675
10	0.90	—	—	27	60	239	957
10	0.95	—	—	—	26	104	415
20	0.85	—	—	34	75	301	1205
20	0.90	—	—	—	38	154	615
20	0.95	—	—	—	—	60	239
20	0.97	—	—	—	—	33	130
20	0.99	—	—	—	—	—	40
30	0.90	—	—	—	32	128	513
30	0.95	—	—	—	—	45	178
30	0.97	—	—	—	—	23	93
30	0.99	—	—	—	—	—	27
40	0.95	—	—	—	—	37	149
40	0.97	—	—	—	—	—	75
40	0.99	—	—	—	—	—	21

^a Sample sizes were computed from (6). Values less than 20 were not presented, because we do not believe it is appropriate to recommend such small sample sizes. Reasons for this belief are: (1) we question the applicability of results relying on asymptotic theory to such small sample sizes; and (2) since (6) involves guesses of p, ET and EY, we feel the resulting uncertainty would never warrant our recommending a sample size of less than 20 nests.

(denote these guesses by p^* , \bar{T}^* , \bar{Y}^*) into (4) and obtain the approximate number of nests, K^* , we need to observe:

$$(6) \quad K^* = \frac{(1 - p^*)^2}{\bar{T}^*(1 - \hat{p})^2 + (\bar{Y}^* - 1)(1 - 2p^*)(cv)^2}$$

In the absence of other estimates of ET or EY we may wish to specify θ_j and p to compute EY and ET in the standard manner using (1). As an example of sample sizes needed to estimate p with various levels of precision, we have computed values of K^* using several reasonable combinations of J and p (Table 3). All values in Table 3 were computed using ET and EY under the assumption that

$$\theta_j = \frac{p^{j-1}(1 - p)}{1 - p^j}, \quad j = 1, 2, \dots, J.$$

Finally, we wish to indicate some uses of the tables for the field biologist. Table 1 shows that when the model assumptions are met and the field biologist uses the approximate confidence interval estimates herein sug-

gested, the actual frequency of coverage is quite close to the theoretical in a wide range of situations. In any one case, however, the estimate of p (and hence also of p^j) can be considerably different from the true value especially when the number of nests in the sample is small (see Max \hat{p} and Min \hat{p} in Table 1). Comparisons of \hat{p}^j and \bar{Y} show that \hat{p}^j is always a better estimate of nesting success when the assumptions of the model obtain, and that the difference in these two estimates is greater in cases of lower overall nesting success.

The precision of the Mayfield estimator in a field situation is of course dependent on how closely the assumptions of the model are met by the population in question. It is doubtful whether this model (or any other probability model of a biological phenomenon for that matter) will reflect exactly the reality of nature. However, the traditional estimator \bar{Y} is almost sure to overestimate nesting success in all situations where nests are found on other than the first day of the nesting period (see for example, Mayfield 1960, 1961, 1975; Custer and Pitelka 1977). If the assumptions of this model approximate the reality of a population, then we suggest its use to correct for the obvious, known bias associated with \bar{Y} . In cases where this model seems totally inappropriate we know of no way to accurately estimate nesting success if nests other than first day nests are to be used.

Table 2 gives empirical estimates of the power in testing the null hypothesis that $p_1 = p_2$ against the alternatives that $p_2 = p_1 + \Delta$. This table gives, for selected values of Δ , the probability of rejecting the null hypothesis given that in fact $p_2 = p_1 + \Delta$. Note that for $\Delta \neq 0$ rejecting the null hypothesis is the correct decision, and hence we would hope the probability of rejecting would be large. For $\Delta = 0$ this probability should be the level of significance α for the test. Table 2 shows how the power function varies with changes in Δ , p_1 , J , and K . A more detailed discussion of the concept of the power of a statistical test can be found in Cohen (1977).

Table 3 is a guide for the field biologist to determine the number of nests needed in his or her sample in order to achieve a given precision in the estimator. We feel that a sample size of at least 20 nests is needed in all cases (our reasons are given in Table 3) so only calculated sample sizes greater than 20 are presented. As mentioned, the biologist must first make guesses of p , EY and ET or of p and θ_j , $j = 1, \dots, J$, in order to calculate the sample size required for a specified coefficient of variation using equation (6). Table 3 covers several cases, but direct calculation using (6) is a simple matter in cases not covered in the table.

SUMMARY

Using a nesting model proposed by Mayfield (1960, 1961, 1975) we show that the estimator he proposes is a maximum likelihood estimator (m.l.e.). M.l.e. theory allows us to calculate

the asymptotic distribution of this estimator, and we propose an estimator of the asymptotic variance. Using these estimators we give approximate confidence intervals and tests of significance for daily survival. Monte Carlo simulation results show the performance of our estimators and tests under many sets of conditions. A traditional estimator of nesting success is shown to be quite inferior to the Mayfield estimator. We give sample sizes required for a given accuracy under several sets of conditions.

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